American Fisheries Society Symposium 87: 2019

Role of Recovering River Herring Alosa spp. Population on Smallmouth Bass Diet and Growth

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Abstract.—Fish assemblages in Atlantic coastal rivers have undergone extensive ecological change in the last two and a half centuries due to human influence, including extirpation of many migratory fish species, such as river herring (*Alosa* spp.) and introduction of nonnative piscivores, notably Smallmouth Bass *Micropterus dolomieu*. Recently, dam removals and fish passage improvements in the Penobscot River, Maine, have allowed river herring to return to reaches of the river that have been inaccessible since the late 19th century. Alosine populations have increased and this trend is anticipated to continue. This may increase forage in the system which could potentially increase growth for Small-

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mouth Bass, the dominant piscivore. We examined the diet and growth of Smallmouth Bass collected from areas of the Penobscot River watershed with and without access to river herring as prey. We collected 765 Smallmouth Bass throughout 2015, examined the stomach contents of 573 individuals, and found notable differences in diet among three river reaches with common seasonal trends. Juvenile river herring composed an average of 19% (SE = ±6%) of stomach contents by mass from Smallmouth Bass collected in the freshwater tidal area but were rarely observed in the diets upstream. We used estimates from von Bertalanffy growth models to examine differences in growth among reaches and found that asymptotic length was the longest (425 mm TL) in the Tidal reach where access to river herring was unrestricted. We then used these data to predict changes to growth associated with increased access to juvenile river herring prey with bioenergetics models. Results indicated that substituting juvenile river herring for less energy-dense prey (e.g., invertebrates) may lead to increases in seasonal growth throughout the watershed as river herring populations continue to rebound in response to dam removal. Our results provide insight into the diet and growth of Smallmouth Bass in a large New England river, and provide a foundation for future work investigating unfolding changes to these characteristics following recent dam removals.

Introduction

Growth and life history patterns of predatory fishes are influenced by prey availability (Adams et al. 1982a; Boisclair and Leggett 1989; Dunlop et al. 2005), prey size (Michaletz 1997; Pazzia et al. 2002), and prey energy density (Rand et al. 1994). Diet composition can influence growth (Boisclair and Leggett 1989) and size at maturity (Shuter et al. 2016) of predators. Differences in diet can result in growth differences across spatial (Yako et al. 2000; Glover and DeVries 2013) and temporal (Martin 1970; Shuter et al. 2016) scales. Therefore, the introduction or restoration of forage fish may result in changes to predator diet and growth. The degree to which seasonal influxes of sea-run forage fishes influence these characteristics in freshwater resident predators is, however, poorly documented.

One such piscivorous fish, the Smallmouth Bass *Micropterus dolomieu*, native to the St. Lawrence and Mississippi drainages (Werner 2004), has been introduced widely throughout the world (Jackson 2002) and has been implicated in declines of abundance and diversity of native minnows, salmonines, and other sensitive taxa (Whittier and Kincaid 1999; Weidel et al. 2007). They also prey upon anadromous fishes in areas outside of their native range such as the Pacific Northwest (e.g., Fritts and Pearsons 2004; Tabor et al. 2007). In Maine, Smallmouth Bass were introduced in the late 19th century and have spread throughout most watersheds since then (Warner 2005). During this period, construction of numerous large dams fragmented habitat and contributed to the decline or extirpation of anadromous fish populations (Saunders et al. 2006). Recently, the Penobscot River in Maine has been the focus of a restoration project, including two large dam removals and upgraded fish passage facilities at several remaining dams. This project is collectively known as the Penobscot River Restoration Project—PRRP (see Opperman et al. 2011 for description).

Anadromous river herring (Alewife *Alosa pseudoharengus* and Blueback Herring *A. aestivalis*), once abundant in the Penobscot River watershed, were at historically low abundances (Saunders et al. 2006) prior to recovery efforts that included dam removal and stocking. These efforts increased connectivity for sea-run fishes, resulting in substantial population growth for anadromous river herring *Alosa* spp. in this system, with returns increasing by more than one million spawning adults in just a few years following dam removal (M. Simpson, Maine Department of Marine Resources, personal communication). This change in prey dynamics has the potential to influence diet and growth of Smallmouth Bass populations in the catchment.

Anadromous river herring can influence resident fishes and freshwater ecosystems via several pathways. Migration of adults and freshwater rearing of juveniles can influence nutrient budgets (Twining et al. 2013) and shift zooplankton communities (Post et al. 2008; Howeth et al. 2013). Both adult and juvenile life stages can provide energy-dense forage for piscivorous fish (Hall et al. 2012). In freshwater they are preyed upon by Largemouth Bass *Micropterus salmoides* (Yako et al. 2000), Blue Catfish *Ictalurus furcatus* (MacAvoy et al. 2000), and other species (Mattocks et al. 2017). Landlocked river herring populations are important prey for Salmonines in the Great Lakes (Stewart and Ibarra 1991; Rand et al. 1994; Savitz 2009), Striped Bass *Morone saxatilis* (Cyterski et al. 2002), and Chain Pickerel *Esox niger* (Brodersen et al. 2015). Other studies (e.g., Yako et al. 2000; Mattocks et al. 2017) have described predation by piscivorous fishes on juvenile anadromous river herring in their natal lentic environments. Notably, Yako et al. (2000) found that juvenile anadromous alewives constituted a large portion of Largemouth Bass diets in Massachusetts lakes with fish growing larger when anadromous river herring were present.

Interactions between anadromous river herring and Smallmouth Bass likely extend beyond that of a predator–prey relationship, but previous studies have produced conflicting results. Hanson and Curry (2005) hypothesized that competition between young-of year (YOY) river herring and Smallmouth Bass might be significant based on diet overlap. In contrast, Willis (2009) noted little diet overlap between these species and observed no difference in Smallmouth Bass condition in lakes with or without river herring. The uncertainty surrounding competition during early life history has influenced policy decisions about fish passage in North America. For example, in the St. Croix River, the eastern border between Maine and New Brunswick, concerns over a perceived decline in Smallmouth Bass abundance prompted the state to close fish passage structures and exclude river herring from natal spawning grounds, although restoring river herring access to historic habitat is a top priority of Native American tribes and New Brunswick provincial fisheries agencies (Willis 2009).

Rebounding populations of river herring are expected to provide an important prey source for Smallmouth Bass, the dominant piscivore the lower Penobscot River watershed (Kiraly et al. 2014; Watson et al. 2018), because juvenile river herring are available as prey throughout the growing season due to extended emigration timing (Iafrate and Oliveira 2008). Rearing and out-migration of anadromous river herring is protracted throughout the summer and fall in the Northeastern United States (Yako et al. 2002), when water temperatures are optimal for Smallmouth Bass consumption (~22°C; Whitledge et al. 2003). Furthermore, Smallmouth Bass living in freshwater tidal areas may benefit from extended access to pulses of juvenile river herring exported from lakes and ponds upstream. Though juveniles are typically thought to migrate directly to the ocean, several studies of river herring have revealed prolonged presence in freshwater tidal waters (e.g., Limburg 1998; Gahagan et al. 2012; Turner and Limburg 2016)

Smallmouth Bass predation on juvenile anadromous river herring in rivers has not been well described, though these interactions have the potential to greatly influence population dynamics of both species. The purpose of this study was to assess diet and growth of Smallmouth Bass, in the context of watershed-scale efforts to recover river herring populations. We used the Penobscot River watershed as a study system to test the extent to which recent increases in river herring populations may influence Smallmouth Bass growth and diet. To do so we (i) assessed the diet of Smallmouth Bass in three river reaches with different access to river herring as prey, (ii) compared growth of Smallmouth Bass among those reaches, and (iii) used a bioenergetics model to determine potential Smallmouth Bass growth under scenarios of increasing consumption of anadromous river herring following projected population increases.

Methods

Collection and Processing

We used three study reaches in the Penobscot River catchment based on river herring presence (both current and historic) and locations relative to several main-stem dams (Kiraly et al. 2014). We collected Smallmouth Bass from two reaches of the Penobscot River (Figure 1), corresponding to strata delineated by Kiraly et al. (2014): (i) Orono, which is currently below the lowermost dam and, as of 2014, was accessible to river herring, and (ii) the Tidal reach, which was freshwater, downstream from the head of tide, and has been historically accessible to “remnant” populations of migratory fishes including river herring (Grote et al. 2014). We also sampled the Piscataquis River (Piscataquis reach), a major tributary to the Penobscot River, which was inaccessible to anadromous river herring during our collections, but supports a regionally valuable Smallmouth Bass fishery. We collected individuals from an additional reach (Argyle) and used those individuals only in growth analyses.

We captured a total of 764 Smallmouth Bass with electrofishing and angling from May to October 2015. We used electrofishing to capture 372 individuals in conjunction with fish community surveys described by Watson et al. (2018). We used angling with curly-tailed grub lures (white, 7.6 cm length) to collect an additional 393 individuals from July until September. We used 572 individuals ranging from 145- to 464-mm TL for stomach analysis, with 72% of those fish captured during summer angling collections. Angling began at sunrise and continued until minimum sample sizes were met or four hours had elapsed. This time was chosen because Smallmouth Bass are crepuscular predators (Reynolds and Casterlin 1976) and water temperatures are lowest at night, which slows digestion. We attempted to collect ten individuals in each 50-mm size-class from each site, starting at 150 mm, in order to obtain a representative range of sizes and diets. For common size classes (e.g., 200–300 mm), we frequently released fish once we met our goal. However, for uncommon sizes (e.g., > 350 mm) or during periods of low catch due to low water temperatures (e.g., October sampling), we did not always meet our catch quotas.

We measured total length (TL) of each fish and, if they met our size criteria, we euthanatized them by lethal overdose with buffered MS-222. The fish were then placed in a cooler with ice water and brought back

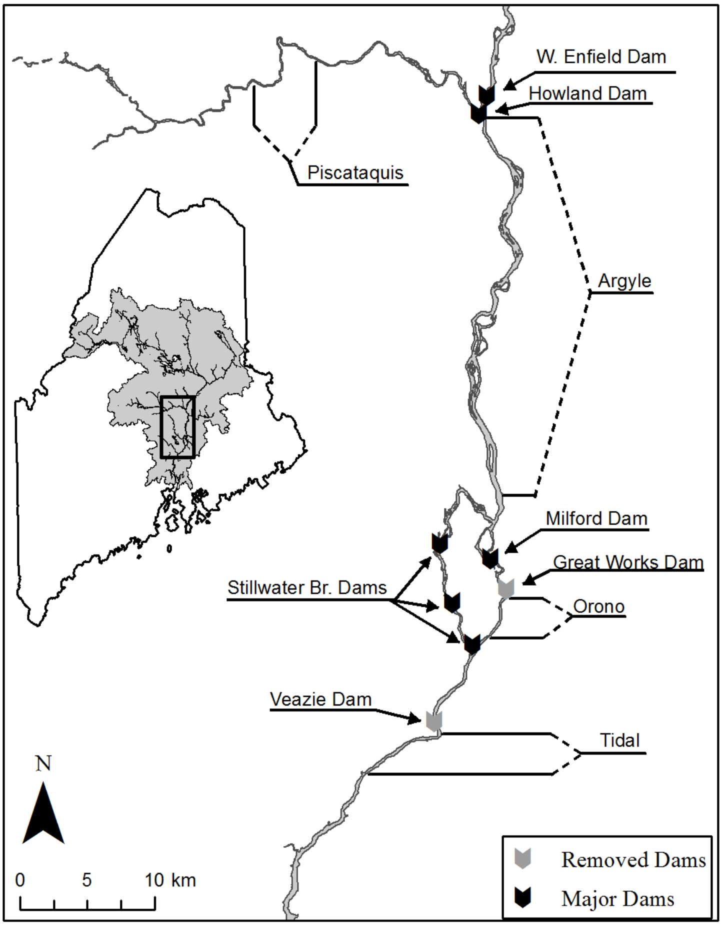

Figure 1. The Penobscot River watershed, Maine (inset) and lower mainstem river including the Piscataquis River. Also included are the locations of dams both present and former and the delineations of the sample reaches where Smallmouth Bass were collected.

to the laboratory for dissection. Upon arrival, fish were dissected immediately or frozen for later dissection. We measured a subset of fish (n = 75) before and after freezing and confirmed total length measurements were not detectably different (two sample t-test, p = 0.43). During dissection, we removed sagittal otoliths and removed stomachs by cutting the esophageal and pyloric sphincters. Stomachs were wrapped in muslin cloth, fixed in a buffered 10% formaldehyde solution for 72 h, rinsed with water, and stored in 70% ethanol before further dissection and sorting.

Diet Analysis

We removed all preserved contents from each stomach and sorted into one of five categories: river herring, other fish, insect, crayfish, and other. Items were classified as “other” if the prey was either unidentifiable or did not fit into one of the other four prey categories. The “insect” prey category included both terrestrial (e.g., caterpillar) and aquatic (e.g., stoneflies) insect species. The “other fish” category included all species other than river herring and unidentifiable fish tissue. The distinctive body form of river herring (i.e., deep bodied, laterally compressed, deeply forked tail) facilitated identification in gut contents. Each prey type from each stomach was then placed in a tared aluminum container and dried at 60°C for 24 h. Dry mass was recorded to the nearest 0.001 g.

We calculated average frequency occurrence (O_i) of each prey type i in each reach j, defined as:

$$O_i = \frac{J_{ij}}{P_j}$$

where J_{ij} was the number of fish containing prey i in reach j and P_j was the number of fish with food in their stomachs in reach j. This measure describes how often each prey type was consumed and compliment measures of prey mass. We also calculated the ratio of the total mass of each prey type (<!–[if gte msEquation (12)] in group j following the ratio estimation procedure detailed by Hansen et al. (2007). Fish were grouped according to collection month and size-class (TL < 224, 225–274, 275–324, and <325 mm TL) in each reach and ratios were calculated as:

$$\hat{R} = \frac{\Sigma_{i=1}^{n} y_{ij}}{\Sigma_{i=1}^{n} x_j}$$

Where y_{ij} was the mass of prey type i in group j and x_j was the total mass of all prey types in group j. The standard error for this ratio (Hansen et al. 2007) was approximated as:

$$\mathrm{SE}\ (\hat{R}) = \frac{1}{\sqrt{n_j}\ \bar{x}_j} \sqrt{\frac{\Sigma_{i=1}^{n} (y_{ij} - \hat{R}x_j)^2}{n_j - 1}}$$

Where n_j is the number of stomachs in group j. Unless otherwise noted, all results of diet study are reported as mean ± SE.

Otolith Preparation

We chose to use sagittal otoliths for aging as opposed to nonlethal aging structures (e.g., scales) to reduce aging error and increase precision for Smallmouth Bass older than age five (Long and Fisher 2011). Otoliths were sectioned along the dorsal-ventral axis and photographed along with an external length standard using a Spot 3.1 camera (SPOT Imaging, Sterling Heights, Michigan) mounted on the trinocular port of a MEIJI Techno EMZ-13TR stereomicroscope. We measured to the distal edge of the most recent annulus along the medial axis and measured total medial radius of each otolith with ImageJ (Schneider et al. 2012) and the ObjectJ plugin (Vischer and Nastase 2015). During digital measuring, we simultaneously viewed the photograph of the sectioned otolith and the corresponding slide of sections from the same otolith using a dissecting microscope to ensure that each annuli and margin were marked appropriately. Each otolith was aged by two independent readers and discrepancies in age determination were reconciled prior to measurement. The measurement of each otolith was assigned a qualitative confidence level (1 through 10, low to high) and only measurements with a confidence level of eight or higher were considered in this analysis.

Growth Modeling

We used the von Bertalanffy growth model (VBGM; von Bertalanffy 1938) to estimate growth curves for fish from each reach. We used the Modified Fry method detailed by Vigliola and Meekan (2009) to estimate length for the most recent annulus to account for the variability in capture dates and corresponding seasonal growth differences. We used size at age data from individuals captured in the three reaches from the diet study: Tidal (n = 166), Orono (n = 257), and Piscataquis (n = 132). We also included size at age data from the Argyle reach (n = 167) to improve parameter estimates, but do not present those results here for brevity.

We fit the VBGM as a Bayesian hierarchical model with a Markov chain Monte Carlo (MCMC) approach in JAGS (Plummer 2003) using the R2jags package (Su and Yajima 2015) in R (R Core Team 2016). We used a hierarchical model specification (see He and Bence 2007) to facilitate information sharing among reaches while allowing separate estimation of VBGM parameters for fish within each reach.

The length of each fish (L_i) at age t_i was estimated using the VBGM as:

$$L_i = L_{\infty j}\,(1 - e^{-K_j(t_i - t_{0j})})$$

where $L_{\infty j}$ was the asymptotic length of fish in each reach j, K_j was the Brody growth coefficient in each reach, and t_{0j} was the age at length zero in each reach.

We used uninformative hyperpriors for all model parameters. We confirmed model convergence using the Gelman-Rubin statistic ($\hat{r} < 1.10$), and by graphical inspection of mixing among chains (Kruschke 2011). Effective sample size was sufficient to construct posterior estimations of all parameters. We assessed differences in growth parameters by calculating the difference in parameter estimates between all paired reaches and assessed statistical significance based on lack of overlap of 95% CRI with zero (Kéry 2010).

Bioenergetics Modeling

We used the Wisconsin mass-balance bioenergetics model (Hanson et al. 1997) and metabolic values reported by Whitledge et al. (2003) to model annual Smallmouth Bass growth under different diet scenarios. We used daily average temperature values from two USGS gauging stations, one on the Piscataquis River and the other on the mainstem Penobscot River (USGS 2016a, 2016b). All models were run for the period in which average water temperatures were greater than 8°C (May 1–October 31). Because Smallmouth Bass are largely inactive, and presumably not feeding below 10°C (Roell and Orth 1993), we assumed that all annual growth would occur during the modeled period, though other studies (e.g., Adams et al. 1982b) have shown that weight loss does occur during winter. We also substituted daily average temperature measurements from the two gauges in the Piscataquis and Tidal reaches to determine whether differences affected estimates.

Modeled diet proportions were taken from individuals with a total length of 225–325 mm at time of capture to avoid the influence of different feeding strategies employed by the largest and smallest fish in our samples. Because 93% of "other" diet items by mass were found in only 4% of stomachs, we excluded these prey types from diet composition in bioenergetics analyses. We interpolated diet proportions for each day between sampling events. Because we did not collect diet samples in May and October in the Piscataquis reach, we estimated diet composition in those months based on seasonal trends observed in the other two reaches.

We ran all models using average prey energy content values reported by Yako et al. (2000) for four prey types: river herring (5.6 kJ/g), other fish (4.1 kJ/g), crayfish (3.2 kJ/g), and insect (3.2 kJ/g). Prey energy content was assumed to be constant throughout the modeling period. Predator energy content was held constant at 4.2 kJ/g (wet mass) through all models, a common assumption for models of centrarchid bioenergetics (Whitledge et al. 2003). We chose to model annual growth for individuals ranging from age 2 to age 5 due to the dominance of those age classes in our samples. We used results from the VBGM and a length-mass relationship ($R^2 = 0.99$) developed for Smallmouth Bass in the Penobscot River watershed (Watson et al. 2018) to estimate seasonal growth in grams.

We first ran models using observed diet data for each reach to produce an estimate of the percent of maximum consumption (%

C_{max}) for each age-class required to achieve average annual growth. Next, we ran a model with proportions of juvenile river herring observed in Orono diets substituted in the Piscataquis reach diets to simulate a relatively modest increase in river herring consumption. Finally, we ran two models with proportions of juvenile river herring observed in diets of Smallmouth Bass captured in the Tidal reach substituted for the diet in both Orono and Piscataquis reaches to simulate large increases in consumption of this prey. Given that estimates calculated by Opperman et al. (2011) for carrying capacity of river herring in this system following restoration efforts are an order of magnitude larger than was observed at the most downstream fishway in 2015, we felt estimates of consumption of river herring in the Tidal reach were reasonable for possible future consumption in upstream reaches. In all instances where diet was manipulated, % C_{max} was held at the rates previously modeled and the proportion of remaining diet items consisted of the observed diets rescaled to represent the proportion of the diet not composed by juvenile river herring.

Results

Diet

Insects were the most frequently consumed prey type in every reach (Table 1), though many fish contained minimal insect matter, which resulted in lower empty stomach occurrence. On average, we found insects in 76% of stomachs that contained prey. Fish were, on average, the next most commonly occurring prey type, and were found in 23% of stomachs containing prey. The proportion of empty stomachs from each sampling occasion ranged from 4% to 33%, with an average of 19% across all sampling occasions. We removed data from fish with empty stomachs from further diet analyses.

Average stomach content mass was highest in the Tidal reach, relative to other reaches and we also found novel prey types. Average dried stomach content mass ranged from 0.39 ± 0.13 g in the Piscataquis reach to 0.57 ± 0.16 g in the Tidal reach and was highly variable among individuals. Items in the "other" prey category composed a large portion of the diets (>20% by mass) in several months due to the occurrence of several large prey items in relatively few individuals. Several novel food items dominated the mass of this category, including three rodents, three frogs, and two juvenile snapping turtles with an average dried mass of 5.5 ± 3.8 g, 2.0 ± 1.2 g, and 2.1 ± 1.0 g, respectively.

Smallmouth Bass consumed juvenile anadromous river herring to a variable extent, depending on availability and location in the watershed. Smallmouth Bass consumed the most river herring in the Tidal reach across all months and size classes. In the Orono reach, river herring were only found in diets during July samples and only in 3% of stomachs. We found river herring in 14% of stomachs con-

Table 1. Average frequency of occurrence (%) of each prey type found in all Smallmouth Bass stomachs containing prey in three sampled reaches of the Penobscot River watershed, Maine.

Reach	River Herring	Other Fish	Crayfish	Insect	Other
Tidal	14	30	8	68	20
Orono	3	18	4	76	19
Piscataquis	0	15	15	83	15

taining prey from the Tidal reach. During the months in which they were available (July–October), juvenile river herring averaged 19 ± 6% of prey by mass in the Tidal reach, 4 ± 1.9% in the Orono reach, and were not found in the stomachs collected in the Piscataquis reach (Figure 2). Consumption of adult river herring was limited to one occurrence in the Tidal reach in May.

River herring were more prevalent in the diets of Smallmouth Bass in the Tidal reach than the upstream reaches. In the Tidal reach, river herring composed 12% to 55% of the diet by mass in each size-class (Figure 2B). Juvenile river herring composed 44 ± 28% of the diet by mass for the smallest size-class (TL < 225 mm) sampled in the Tidal reach. In contrast, the diet proportion by mass of the

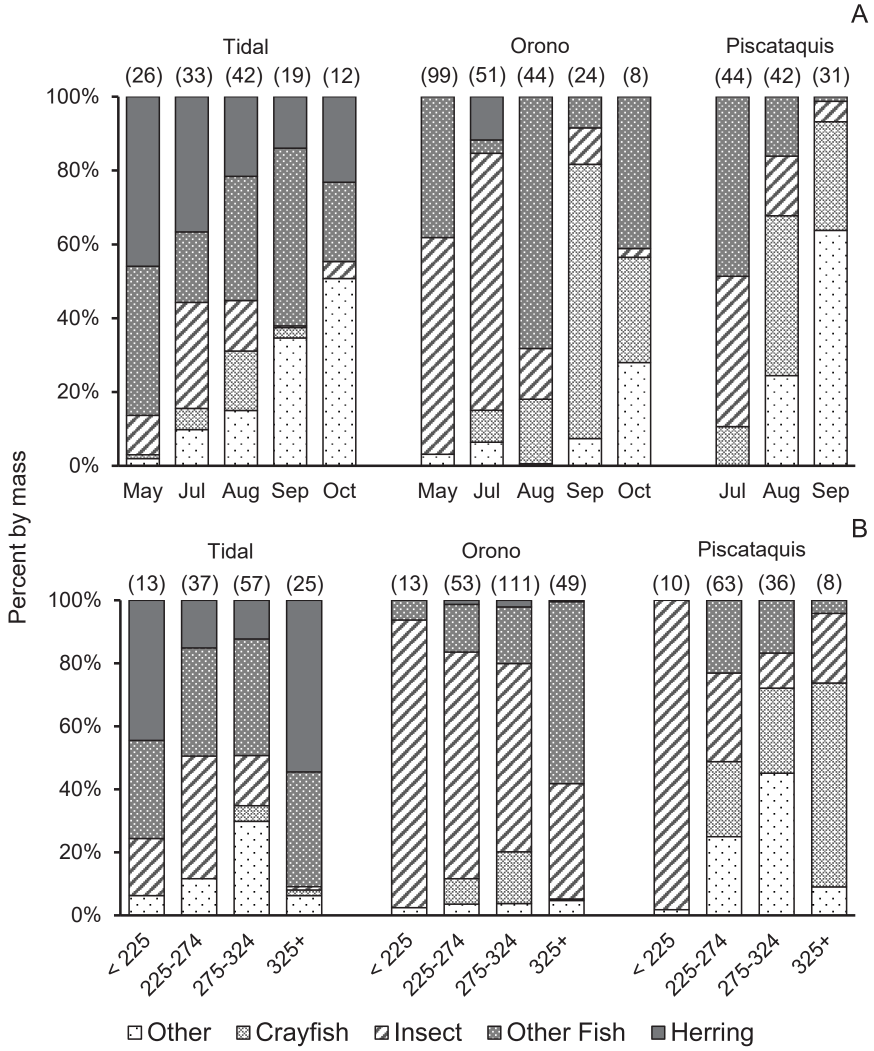

Figure 2. Percent diet composition by mass (g) of Smallmouth Bass reported by month (A) and 50-mm size-class (B) in three different reaches (Tidal, Orono, Piscataquis) of the Penobscot River watershed, Maine. The number of stomachs containing prey items in each sample is shown in parentheses above each bar.

smallest size-class in the other two reaches was dominated by insects, with their contribution decreasing in larger size classes. The contribution of other fish to the diets of different size classes of Smallmouth Bass in the Tidal reach remained relatively consistent, ranging from 31 ± 20% to 37 ± 13% by mass. In the Orono reach, other fish composed the largest portion of the diet by mass (R = 58 ± 13%) for the largest size-class (≥325 mm TL). In the Piscataquis reach, crayfish composed the largest portion of the diet by mass in the largest size-class (R = 65 ± 21%).

We also observed more insects in diets across reaches earlier in the growing season followed by increasing proportions of different prey types. Insects composed the largest observed proportion by mass in July for each reach and decreased in the proceeding months (Figure 2A). We also found “other” prey items increasing in relative proportion throughout the sampling period, primarily due to large individual prey items during September and October sampling periods.

Otolith Analysis and Growth Modeling

We used back calculations from a total of 722 otoliths to fit the hierarchical VBGM. Of a total of 765 otoliths processed, we assigned low confidence ratings to 24 measurements, and they were omitted from further analysis. An additional 19 otoliths were collected from age-0 fish and were only used to inform back-calculations. Smallmouth Bass grew to the largest asymptotic length in the Tidal reach (Table 2) and length-at-age varied accordingly (Figure 3). As confirmation of this trend, we observed only a modest difference in average asymptotic size among reaches, with the largest difference (3.6 cm) occurring between the Tidal and Orono reaches. Other VBGM parameter estimates (K, t_0) were not significantly different between reaches. Interestingly, we observed fish up to age 20 in the Orono reach, but only age 13 and 10 in the Piscataquis and Tidal reaches, respectively.

Bioenergetics Modeling

Estimates of % C_{max} decreased with age and ranged from 0.4 to 0.9 across modeled ages in all reaches using observed diet data. Average observed temperature was lower in the Piscataquis reach (17.4°C) than the Tidal reach (18.6°C) during the modeled period, though these differences did not result in large changes to estimated growth (≤5% ending mass difference) when temperature data were substituted among reaches with estimated consumption rates held constant.

When we substituted the river herring-rich diet observed in the Tidal reach into diets of fish in Orono and Piscataquis reaches (holding consumption rates constant) we simulated that seasonal growth would increase substantially (Figure 4). Increased river herring in the diet for the Piscataquis and

Table 2. Pairwise comparisons of the difference in posterior distributions of maximum length (L_∞) and associated 95% credible intervals (CRI) among three reaches (Tidal, Orono, Piscataquis) of the Penobscot River catchment, Maine USA.

Comparison	Mean difference	Lower 95% CRI	Upper 95% CRI
Orono - Piscataquis	–4.02	–32.80	16.16
Orono - Tidal *	–36.59	–71.88	–14.19
Piscataquis - Tidal *	–32.57	–60.65	–7.09

*Indicates statistical significance ($\alpha < 0.05$)

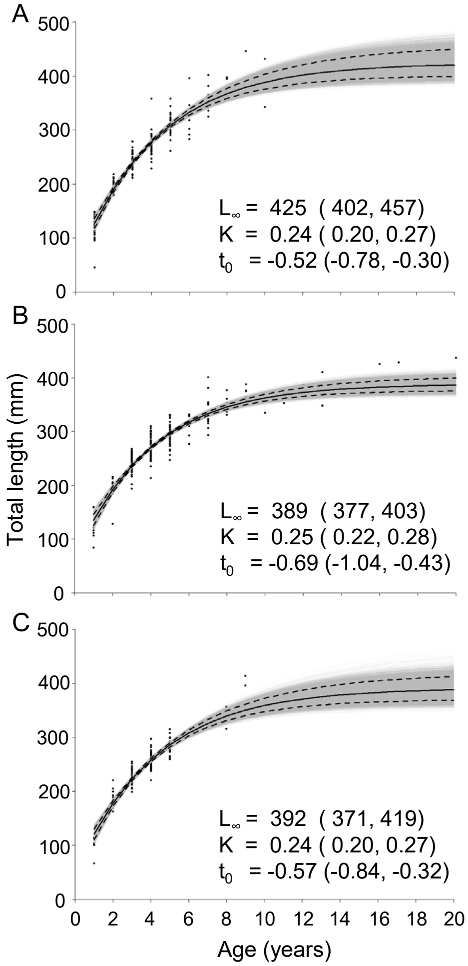

Figure 3. Posterior predictions from von Bertalanffy growth models fit to back-calculated size-at-age data for Smallmouth Bass in the Tidal (A), Orono (B), and Piscataquis (C) reaches of the Penobscot River, Maine. Points represent raw data, gray lines represent posterior predictive von Bertalanffy growth model (VBGM) curves, black solid lines represent average posterior predictive VBGM curves, and the dashed lines represent the 95% credible interval. Upper and lower 95% credible intervals are provided in parentheses next to each estimated growth parameter.

Orono reaches resulted in a modeled average seasonal growth increase of 35% and 31% by mass, respectively. In contrast however, substituting the lower observed prevalence of river herring found in the Orono diet into the Piscataquis diet resulted in a moderate increase in growth, with an average increase of 7% by mass across age classes. It is important to note that assumptions made about consumption are a substantial source for errors in growth estimates (Bajer et al. 2004), so results from this model represent only an estimate of possible future growth.

Estimates of % C_{max} were influenced by the diet energy density. We estimated that fish in the Piscataquis reach fed at the highest rate, followed by the Orono and Tidal reaches, respectively. This is likely because Smallmouth Bass in the Piscataquis reach ate primarily insects and crayfish, which have

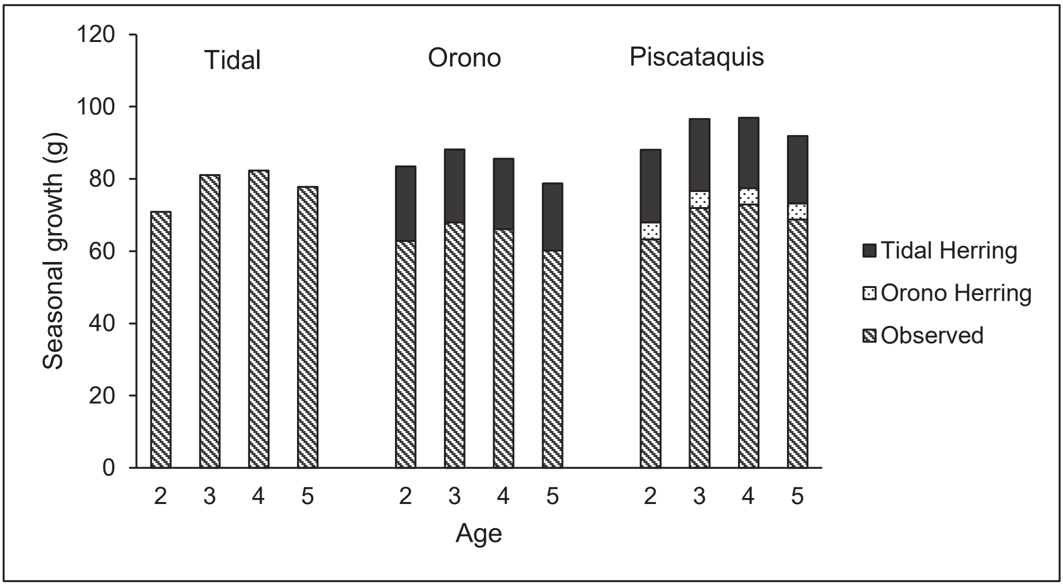

Figure 4. Observed and predicted seasonal growth (g) of Smallmouth Bass ages 2–5 in three reaches (Tidal, Orono, Piscataquis) of the Penobscot River watershed, Maine. Growth was predicted for two separate bioenergetics models (Tidal Herring, Orono Herring) under conditions of increased availability of river herring prey for restored reaches. The Tidal Herring model substituted proportions of river herring in the diet from the Tidal reach into the diets of the two upstream reaches. The Orono Herring model substituted the modest consumption of river herring in the Orono reach into the diet of the Piscataquis reach. Consumption, prey energy density, and metabolic rates were held constant for model predictions.

a relatively low energy density. In contrast, diets in the Tidal reach are composed primarily of fish (including river herring) which are more energy-dense. Thus, Smallmouth Bass in this reach are estimated to feed at a lower rate, because they consume more energy-dense prey and have similar seasonal growth relative to the other reaches.

Discussion

Our study demonstrates that Smallmouth Bass feed upon energy-dense juvenile anadromous river herring in the Tidal reach, which may contribute to modestly larger asymptotic size. Smallmouth Bass appear to feed upon these prey when they are available and abundant, though we found river herring in only 3% of Smallmouth Bass stomachs in the Orono reach during the early stages of restoration. Bioenergetics models indicated that substituting river herring in place of less energy-dense prey results in increased seasonal growth potential, but empirical growth estimates (K) did not vary significantly among reaches with varying levels of access to river herring, which may have potentially been associated with differences in consumption and habitat. These data were collected in two years following dam removals and fish passage improvement when adult anadromous river herring returns at the lowermost dam were approximately 15% of the potential abundance (Opperman et al. 2011). Thus, this study provides a valuable baseline for Smallmouth Bass growth and utilization of anadromous river herring as abundance of alosine species is projected to increase further.

Several studies have described diet patterns of stream-dwelling Smallmouth Bass similar to those detailed here, including decreasing importance of insects in the diet of older fish (Roell and Orth 1993) and later in the growing season (Probst et al. 1984). These studies also indicate that crayfish comprise the majority of the diet among older fish. This was the case in our most upriver site (Piscataquis) but fish (including river herring) comprised the largest portion of the diet in the Tidal reach (across all sizes). These differences in diet may forecast upstream changes in Smallmouth Bass growth patterns as river herring populations continue to increase.

Our study contributes to a growing body of evidence that river herring may provide an important source of forage for resident freshwater piscivores which may impact their growth and abundance. Fish that consume larger or more energy-dense prey grow faster (Martin 1970; Boisclair and Leggett 1989) and have higher winter survival (Shuter and Post 1990). River herring are an energy-dense forage fish relative to other prey types (Adams et al. 1982b; Cyterski et al. 2002), and similar studies have shown that piscivores prey on seasonally available, energy-dense clupeids in various freshwater systems (Yako et al. 2000; Cyterski et al. 2002; Trippel et al. 2015). Yako et al. (2000) attributed larger asymptotic size of Largemouth Bass in lakes to the presence of juvenile anadromous Alewife. In this study, we estimated the largest asymptotic length for Smallmouth Bass in the Tidal reach, which may be associated with a persistent, albeit remnant population of river herring in that area. Brodersen et al. (2015) observed that Chain Pickerel also preyed extensively on landlocked Alewife and, as a result, exhibited greater lipid content than their counterparts in lakes without Alewife.

Juvenile anadromous river herring exhibit multiple, distinct emigration events from natal habitats (Iafrate and Oliveira 2008; Turner and Limburg 2016) throughout the summer, coinciding with the growing season of Smallmouth Bass. These migration timings may have limited our ability to detect juveniles in Smallmouth Bass diets in upstream reaches where swift stream flows expedite out-migration. In this study, freshwater tidal areas seemed to present the largest opportunity for predator–prey overlap. Other studies of river herring out-migration patterns (Limburg 1998; Turner and Limburg 2016) have described the protracted presence of river herring in tidal areas throughout the late summer and early fall, which may present piscivores in these habitats with additional forage.

In this study, most VBGM parameter estimates were similar between reaches and were comparable to the growth standard reported by Jackson et al. (2008). Relative to this standard, our parameterization of the VBGM produced estimates that were above the mean value (75 percentile) for ages 1 and 2 but below the mean value (25 percentile) for ages older than 3 in all modeled reaches despite similar growth coefficient estimates ($K \approx 0.2$). Similarly, Jackson et al. (2008) reported a standard L_∞ estimate of 499 mm TL for Smallmouth Bass, which is greater than the upper bounds of the 95% CRI estimated for any reaches modeled here. Slower growth at older ages estimated in this study may be the result of Smallmouth Bass growth in a colder climate, where winter mortality is higher for smaller individuals and growth is slower (Beamesderfer and North 1995).

Diet is likely a contributing factor to the differences in estimated maximum length among sites, though other ecological mechanisms are also likely to be causal. Rennie et al. (2009) demonstrated that a suite of biological (e.g., prey availability, predator density) and environmental (e.g., temperature, habitat) factors must be considered to determine the impact of food web changes on resident fish. For example, population density constrains growth rates of individuals (Lorenzen and Enberg 2002; Dunlop et al. 2005). While we made no direct measure of Smallmouth Bass population densities in this study, both Kiraly et al. (2014) and Watson et al. (2018) observed the highest biomass caught per unit effort in the Orono reach with lower densities in the remaining two reaches. Furthermore, the Tidal reach may present conditions more favorable for larger fish (e.g., slower current velocities).

River herring populations in the Penobscot River have only recently rebounded following a major effort to restore river connectivity. It is important to note that we described the growth of Smallmouth Bass in the upper reaches (i.e., Orono, Piscataquis) when the adult river herring returns were beginning to rebound due to stocking efforts and increasing river connectivity. The year we sampled Smallmouth Bass diets (2015) was only the second year after dam removal. Adult river herring returns counted at the lowermost dam were above 100,000 individuals in 2015 (M. Simpson, Maine Department of Marine Resources, personal communication). However, that number more than doubled in 2016, and will likely continue to increase. By 2017 the river herring run exceeded 1.2 million adult fish upstream of Milford Dam. The carrying capacity of river herring for the Penobscot River is estimated to be more than 4 million returning adults (Opperman et al. 2011). Therefore, the changes in growth we anticipate to be associated with changing diets upriver would likely take several years to be detectable through length at age analysis in Smallmouth Bass.

Our bioenergetics models exhibit a positive relationship between river herring consumption and seasonal growth, and it is important to note that these models are limited in their ability to forecast growth under different diet scenarios, especially when accounting for seasonal prey availability (Chipps and Wahl 2008). Thus, results of our bioenergetics model should be interpreted within the context of our assumptions (constant consumption, prey energy density, metabolism). Because we estimated that consumption varied between reaches and metabolism likely varies with habitat and flow, these assumptions were not strictly met and our ability to accurately estimate future growth is limited. Predator–prey interactions are also inherently complex and there are several factors in this study that limit our ability to accurately predict Smallmouth Bass growth in the presence of increasing anadromous river herring availability. Though restoring connectivity for anadromous river herring can be a source of forage for resident fish (Mattocks et al. 2017), other studies have indicated that introduction may create interspecific competition with juvenile sportfish for planktonic prey (Hanson and Curry 2005; Creque and Czesny 2012). Although there are uncertainties about predator–prey interactions, we anticipate that recovering river herring populations will increase growth potential of Smallmouth Bass.

Acknowledgments

We thank L. Katz, G. Innes, D. Whitaker, and numerous students from the University of Maine for field and laboratory assistance. We thank R. Peabody for land access. This work is based upon research supported in part by the Penobscot River Restoration Trust and the University of Maine Department of Wildlife, Fisheries, and Conservation Biology. The U.S. Geological Survey Maine Cooperative Fish and Wildlife Research Unit provided logistical support. The views expressed herein are those of the author(s) and do not necessarily reflect the views of the Penobscot River Restoration Trust, or any of their members. This research was performed under subpermit from the U.S. Fish and Wildlife Service Section 10(a)(1)(A) Permit #TE-697823, Maine Department of Inland

Fish and Wildlife Scientific Collections Permit, and University of Maine approved Institutional Animal Care and Use Committee Protocol Number A2014–08–04. This is the Maine Agriculture and Forest Experiment Station Publication Number 3574, the University of Maine, Orono, Maine, USA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Adams, S. M., R. B. McLean, and M. M. Huffman. 1982a. Structuring of a predator population through temperature-mediated effects on prey availability. Canadian Journal of Fisheries and Aquatic Sciences 39:1175–1184.

Adams, S. M., R. B. Mclean, and J. A. Parrotta. 1982b. Energy partitioning in Largemouth Bass under conditions of seasonally fluctuating prey availability. Transactions of the American Fisheries Society 111:549–558.

Bajer, P. G., G. W. Whitledge, R. S. Hayward. 2004. Widespread consumption-dependent systematic error in fish bioenergetics models and its implications. Canadian Journal of Fisheries and Aquatic Sciences 61:2158–2167.

Beamesderfer, R., and J. North. 1995. Growth, natural mortality, and predicted response to fishing for Largemouth Bass and Smallmouth Bass populations in North America. North American Journal of Fisheries Management 15:688–704.

Boisclair, D., and W. C. Leggett. 1989. Among-population variability of fish growth: II. influence of prey type. Canadian Journal of Fisheries and Aquatic Sciences 46:468–482.

Brodersen, J., J. G. Howeth, and D. M. Post. 2015. Emergence of a novel prey life history promotes contemporary sympatric diversification in a top predator. Nature Communications 6:1–9.

Chipps, S. R., and D. H. Wahl. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. Transactions of the American Fisheries Society 137:298–313.

Creque, S. M., and S. J. Czesny. 2012. Diet overlap of non-native Alewife with native Yellow Perch and Spottail Shiner in nearshore waters of southwestern Lake Michigan, 2000–2007. Ecology of Freshwater Fish 21:207–221.

Cyterski, M., J. Ney, and M. Duval. 2002. Predator demand for clupeid prey in Smith Mountain Lake, Virginia. Fisheries Research 59:1–16.

Dunlop, E. S., J. A. Orendorff, B. J. Shuter, F. H. Rodd, and M. S. Ridgway. 2005. Diet and divergence of introduced Smallmouth Bass (*Micropterus dolomieu*) populations. Canadian Journal of Fisheries and Aquatic Sciences 62:1720–1732.

Fritts, A. L., and T. N. Pearsons. 2004. Smallmouth Bass predation on hatchery and wild salmonids in the Yakima River, Washington. Transactions of the American Fisheries Society 133:880–895.

Gahagan, B. I., J. C. Vokoun, G. W. Whitledge, and E. T. Schultz. 2012. Evaluation of otolith microchemistry for identifying natal origin of anadromous river herring in Connecticut. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:358–372.

Glover, D. C., and D. R. DeVries. 2013. Growth of Largemouth Bass in a dynamic estuarine environment: an evaluation of the relative effects of salinity, diet, and temperature. Canadian Journal of Fisheries and Aquatic Sciences 501:485–501.

Grote, A. B., M. M. Bailey, J. D. Zydlewski, and J. E. Hightower. 2014. Multibeam sonar (DIDSON) assessment of American Shad (*Alosa sapidissima*) approaching a hydroelectric dam. Canadian Journal of Fisheries and Aquatic Sciences 71:545–558.

Hall, C. J., A. Jordaan, and M. G. Frisk. 2012. Centuries of anadromous forage fish loss: consequences for ecosystem connectivity and productivity. BioScience 62:723–731.

Hansen, M. J., T. D. Beard Jr., and D. B. Hayes. 2007. Sampling and experimental design. Pages 51–120 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. Kitchell. 1997. Fish Bioenergetics 3.0. Technical report WISCU-T- 97–001. Madison, Wisconsin.

Hanson, S. D., and R. A. Curry. 2005. Effects of size structure on trophic interactions between age-0 Smallmouth Bass and juvenile anadromous Alewives. Transactions of the American Fisheries Society 134:356–368.

He, J., and J. Bence. 2007. Modeling annual growth variation using hierarchical Bayesian and the von Bertalanffy growth function, with application to Lake Trout in southern Lake Huron. Transactions of the American Fisheries Society 136:318–330.

Howeth, J. G., J. J. Weis, J. Brodersen, E. C. Hatton, and D. M. Post. 2013. Intraspecific phenotypic variation in a fish predator affects multitrophic lake metacommunity structure. Ecology and Evolution 3:5031–5044.

Iafrate, J., and K. Oliveira. 2008. Factors affecting migration patterns of juvenile river herring in a coastal Massachusetts stream. Environmental Biology of Fishes 81:101–110.

Jackson, D. A. 2002. Ecological effects of *Micropterus* introductions: the dark side of black bass. Pages 221–232 *in* D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Jackson, Z. J., M. C. Quist, and J. G. Larscheid. 2008. Growth standards for nine North American fish species. Fisheries Management and Ecology 15:107–118.

Kiraly, I. A., S. M. Coghlan Jr., J. Zydlewski, and D. Hayes. 2014. An assessment of fish assemblage structure in a large river. River Research and Applications 31(3). DOI: 10.1002/rra2738.

Kéry, M. 2010. Introduction to WinBUGS for ecologists: A Bayesian approach to regression, ANOVA, mixed models and related analyses. Academic Press, Upper Saddle River, New Jersey.

Kruschke, J. K. 2011. Doing Bayesian data analysis: a tutorial with R and BUGS. Academic Press, San Diego, California.

Limburg, K. E. 1998. Anomalous migrations of anadromous herrings revealed with natural chemical tracers. Canadian Journal of Fisheries and Aquatic Sciences 55:431–437.

Long, J. M., and W. L. Fisher. 2011. Precision and bias of Largemouth, Smallmouth, and Spotted Bass ages estimated from scales, whole otoliths, and sectioned otoliths. North American Journal of Fisheries Management 21:636–645.

Lorenzen, K., and K. Enberg. 2002. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. Proceedings of the The Royal Society B 269:49–54.

MacAvoy, S. E., S. A. Macko, S. P. McIninch, and G. C. Garman. 2000. Marine nutrient contributions to freshwater apex predators. Oecologia 122:568–573.

Martin, N. V. 1970. Long-term effects of diet on the biology of the Lake Trout and the fishery in Lake Opeongo, Ontario. Journal of the Fisheries Research Board of Canada 27(69):125–146.

Mattocks, S., C. J. Hall, and A. Jordaan. 2017. Damming, lost connectivity, and the historical role of anadromous fish in freshwater ecosystem dynamics. BioScience 67:713–728.

Michaletz, P. H. 1997. Influence of abundance and size of age-0 Gizzard Shad on predator diets, diet overlap, and growth. Transactions of the American Fisheries Society 126:101–111.

Opperman, J. J., J. Royte, J. Banks, L. R. Day, and C. Apse. 2011. The Penobscot River, Maine, USA: a basin-scale approach to balancing power generation and ecosystem restoration. Ecology and Society 16(3):7.

Pazzia, I., M. Trudel, M. Ridgway, and J. B. Rasmussen. 2002. Influence of food web structure on the growth and bioenergetics of Lake Trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59:1593–1605.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *In* K. Hornik, F. Leisch, and A. Zeileis, editors. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22, Vienna, Austria.

Post, D. M., E. P. Palkovacs, E. G. Schielke, and S. I. Dodson. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. Ecology 89:2019–2032.

Probst, W. E., C. F. Rabeni, W. G. Covington, and R. E. Marteney. 1984. Resource use by stream-dwelling Rock Bass and Smallmouth Bass. Transactions of the American Fisheries Society 113:283–294.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Rand, P. S., B. F. Lantry, R. O'Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: implications for Salmonine energetics. Transactions of the American Fisheries Society 123:519–534.

Rennie, M. D., W. G. Sprules, and T. B. Johnson. 2009. Factors affecting the growth and condition of Lake Whitefish (*Coregonus clupeaformis*). Canadian Journal of Aquatic Sciences 66:2096–2108.

Reynolds, W. W., and M. E. Casterlin. 1976. Activity rhythms and light intensity preferences of *Micropterus salmoides* and *M . dolomieui*. Transactions of the American Fisheries Society 105:400–403.

Roell, M. J., and D. J. Orth. 1993. Trophic basis of production of stream-dwelling Smallmouth Bass, Rock Bass, and Flathead Catfish in relation to invertebrate bait harvest. Transactions of the American Fisheries Society 122:46–62.

Saunders, R., M. A. Hachey, and C. W. Fay. 2006. Maine's diadromous fish community: past, present, and implications for Atlantic Salmon recovery. Fisheries 31:537–547.

Savitz, J. 2009. Diets of Lake Michigan salmon and maximum size of Alewife prey. Journal of Freshwater Ecology 24:563–566.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Shuter, B. J., H. C. Giacomini, D. De Kerckhove, and K. Vascotto. 2016. Fish life history dynamics: shifts in prey size structure evoke shifts in predator maturation traits. Canadian Journal of Fisheries and Aquatic Sciences 73:693–708.

Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314–336.

Stewart, D. J., and M. Ibarra. 1991. Predation and production by Salmonine fishes in Lake Michigan, 1978–88. Canadian Journal of Fisheries and Aquatic Sciences 48:909–922.

Su, Y., and M. Yajima. 2015. R2jags: Using R to run 'JAGS'. R package version 0.5–7. Available: https://CRAN.R-project.org/package=R2jags. (September 2018).

Tabor, R. A., B. A. Footen, K. L. Fresh, M. T. Celedonia, F. Mejia, D. L. Low, and L. Park. 2007. Smallmouth Bass and Largemouth Bass predation on juvenile Chinook Salmon and other Salmonids in the Lake Washington basin. North American Journal of Fisheries Management 27:1174–1188.

Trippel, N. A., M. S. Allen, and R. S. McBride. 2015. Importance of resident and seasonally transient prey to Largemouth Bass in the St. Johns River, Florida. Transactions of the American Fisheries Society 144:140–149.

Turner, S. M., and K. E. Limburg. 2016. Juvenile river herring habitat use and marine emigration trends: comparing populations. Oecologia 180:77–89.

Twining, C. W., D. C. West, and D. M. Post. 2013. Historical changes in nutrient inputs from humans and anadromous fishes in New England's coastal watersheds. Limnology and Oceanography 58:1286–1300.

USGS (U.S. Geological Survey). 2016a. National Water Information System data available on the World Wide Web (USGS Water Data for the Nation). Available: http://waterdata.usgs.gov/nwis/uv?01031500. (September 2018).

USGS (U.S. Geological Survey). 2016b. National Water Information System data available on the World Wide Web (USGS Water Data for the Nation). Available: http://waterdata.usgs.gov/nwis/uv?01036390. (September 2018).

Vigliola, L., and M. G. Meekan. 2009. The back-calculation of fish growth from otoliths. Pages 174–211 *in* B. S. Green, B. D. Mapstone,

G. Carlos, and G. A. Begg, editors. Tropical fish otoliths: information for assessment, management and ecology. Springer, New York.

Vischer, N. and S. Nastase. 2015. ObjectJ: Non-destructive marking and linked results. Version 1.03s. Available: http://sils.fnwi.uva.nl/bcb/objectj/. (September 2018).

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biology 10(2):181–213.

Warner, K. 2005. Smallmouth Bass introductions in Maine. Fisheries 30(11):20–26.

Watson, J. M., S. M. Coghlan, J. Zydlewski, D. B. Hayes, I. A. Kiraly. 2018. Dam removal and fish passage improvement influence fish assemblages in the Penobscot River, Maine. Transaction of the American Fisheries Society 147:525–540.

Weidel, B. C., D. C. Josephson, and C. E. Kraft. 2007. Littoral fish community response to Smallmouth Bass removal from an Adirondack lake. Transactions of the American Fisheries Society 136:778–789.

Werner, R. G. 2004. Freshwater fishes of the northeastern United States. Syracuse University Press, Syracuse, New York.

Whitledge, G. W., R. S. Hayward, R. D. Zweifel, and C. F. Rabeni. 2003. Development and laboratory evaluation of a bioenergetics model for subadult and adult Smallmouth Bass. Transactions of the American Fisheries Society 132:316–325.

Whittier, T. R., and T. M. Kincaid. 1999. Introduced fish in northeastern USA lakes: regional extent, dominance, and effect on native species richness. Transactions of the American Fisheries Society 128:769–783.

Willis, T. V. 2009. How policy, politics, and science shaped a 25-year conflict over Alewife in the St. Croix River, New Brunswick-Maine. Pages 793–811 *in* A. J. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjack, J. E. Cooper, K. L. Beal, and T. S. Avery, editors. Challenges for diadromous fishes in a dynamic global environment. American Fisheries Society, Symposium 69. Bethesda, Maryland

Yako, L. A., M. E. Mather, and F. Juanes. 2000. Assessing the contribution of anadromous herring to Largemouth Bass growth. Transactions of the American Fisheries Society 129:77–88.

Yako, L. A., M. E. Mather, and F. Juanes. 2002. Mechanisms for migration of anadromous herring: an ecological basis for effective conservation. Ecological Applications 12:521–534.